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Comparisons of habitat types and host tree species across a threatened Caribbean orchid's core and edge distribution

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Abstract

Tropical forest ecosystems are rich in epiphytes that make up a significant portion of the overall plant diversity. However, epiphytic plants are often understudied due to inaccessibility and the lack of basic ecological information poses challenges to their conservation, particularly in a time of rapid global change. The mule-ear orchid, *Trichocentrum undulatum* (Orchidaceae), is a large flowering epiphyte found in southern Florida (USA), the Greater, and Lesser Antilles including Cuba. The plant is Florida state-listed as endangered with only one remaining small and declining population in a coastal mangrove forest due to historical extraction and habitat destruction. Currently, there is no systematic understanding of the species' habitat requirements. To fill this void, we compared the habitat and microhabitat of the species on its northern distribution edge (southern Florida) and the core range (in Cuba). The Florida population has only one host species, *Conocarpus erectus*, found in one habitat type. This is in sharp contrast to the 92 documented hosts and 5 habitats across 8 provinces in Cuba. Based on our findings from Cuba, we suggest conservation and restoration options in Florida by proposing potential suitable host plants and habitats. Proactive restoration of this species will help to ease the threat from sea-level rise to the species by securing and expanding range margins.

Introduction

Epiphytic plants constitute a significant proportion of the biodiversity in tropical forests (Gentry and Dodson 1987, Kress 1989). However, they are often understudied due to accessibility issues and lack of resources. The absence of basic ecological information, e.g. habitat requirements, poses challenges in conserving epiphytes, particularly in a time of rapid global change. There is a need to plan population translocations to counter current and anticipated future threats, as is done with some endangered plants worldwide (Liu *et al.* 2015, Liu *et al.* 2020, Maschinski and Haskins 2012). The success of such actions depends on understanding the habitat limitations for the species of concern. For example, a good understanding of host species requirements can be used to inform the conservation strategy of threatened epiphytic species (Benzing 1978, Callaway *et al.* 2002, Segovia-Rivas *et al.* 2018, Yang *et al.* 2017). Studies of this kind are rare in the tropics, especially on orchids, one of the most diverse plant families among tropical plants.

Throughout a species' range, there exists a spectrum of habitats, defined by the species' degree of dependence on various biotic and abiotic factors, including the nature and quality of species interactions (Cassini 2013, HilleRisLambers *et al.* 2013, Louthan *et al.* 2015, Parmesan 2006). When species are threatened, conservation strategies depend on understanding those sustaining factors and also anticipating potentially rapid landscape changes (Katina *et al.* 2009, Seddon *et al.* 2013). As one nears the edge of a species' distribution, habitat quality may decline until the distribution "limit" for the species is reached (Sexton *et al.* 2009). Distribution edges can include large swaths of habitat types, elevations, and climate zones extending across latitudes.

Southern Florida lies at the northern edge of the distribution for many tropical plant species, orchids included, that have their core range in the Caribbean or tropical America (Nieto-Blázquez *et al.* 2017, Santiago-Valentin & Olmstead 2004, Trejo-Torres & Ackerman 2001). The subtropical climate of southern Florida may not be as ideal for tropical species, but the varied transitional climate may be tolerable, due to tropical seasonality, despite occasional frost events (Downing *et al.* 2016, Obeysekera *et al.* 1999). The northward movement of species from the Caribbean and tropical America to southern Florida has already been documented for species with strong dispersal capability naturally (Paulson 2001) or aided by human activities

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(Pemberton & Liu 2007, Pemberton & Liu 2008a,b, Skov & Wiley 2005), and it is likely that more species will follow suit. For endangered species that have limited dispersal abilities, or small populations at the limit of a distribution, range shift or expansion into nearby unoccupied yet desirable habitat may be difficult (Liu *et al.* 2012, Martin 2001). Under such circumstances, a conservation strategy might be used to identify suitable habitats for assisted dispersal, which should enhance the probability of establishment and reproductive success (Münzbergová *et al.* 2004).

The dust-like wind-dispersed seeds of orchids may readily disperse to great distances, but can be site-limited due to their dependencies on mycorrhizae for germination and other periods of their life histories (McCormick & Jacquemyn 2014, Yang *et al.* 2017). Determination of host tree diversity and substrate specificity for epiphytic orchids is a critical component to understanding their life histories and habitat suitability as a baseline for conservation planning (Adhikari *et al.* 2012, Ilves *et al.* 2016, Laube & Zotz 2006, Migenis & Ackerman 1993, Mújica *et al.* 2018, Tremblay *et al.* 1997a, Xiqiang 2005). Comparison of host identities and associated plant communities between the core and edge distribution of an orchid species may offer insight into the limiting factors along with its distribution range. The goals of this study are to: (a) identify host trees of *Trichocentrum undulatum* (Sw.) Ackerman & M.W.Chase in the core range area, i.e. Cuba; (b) compare and contrast host plant community types in Cuba and in southern Florida, the species' northern distribution edge; and (c) identify potential suitable but unoccupied habitats for *T. undulatum* in southern Florida where the species is highly threatened with extinction.

Study species

Trichocentrum undulatum is an epiphytic orchid with a distribution in the Greater and Lesser Antilles and southern Florida of the United States (Cetzal-Ix *et al.* 2016). The orchid can be found throughout the entirety of the island country of Cuba and in historically large numbers in Jamaica, with these two islands being the core range in the Caribbean (Ackerman 2014, Ackerman & Chase 2001). Current conservation status of the species in Jamaica is unknown, but populations were reported in decline following high levels of wild harvest and habitat destruction (NEPA 2007). Only one population is currently known to persist in the USA, and it is limited to a thin coastal stretch on the southernmost border of peninsular Florida. Southern Florida is considered the northern latitudinal limit of the species. Throughout the entire distribution of this species, it is subject to anthropogenic threats such as habitat alteration, destruction, collection, and natural forces like hurricanes and specialized herbivory (Borrero *et al.* 2018, Gann *et al.* 2009).

Study site

Populations of *T. undulatum* were studied across the species core range on the island of Cuba as well as the leading northern edge of the species distribution in southern Florida, USA. Cuba, the largest of the Caribbean islands, is home to over 312 orchid species and is thought to be the centre of radiation for many wind-dispersed plant species like orchids and bromeliads (Ackerman 2014). Due to Cuba's geological age, as well as its mountainous landscape, there are diverse habitats and microclimates from which these wind-dispersed species can spread (Borhidi & Muñiz 1985, Nieto-Blázquez *et al.* 2017). In contrast, the Everglades National Park (ENP) is lower in elevation than much of Cuba, ranging from 0 to 2.4-m above sea level. The ENP is the largest wetland preserve in the USA covering over 64,238 ha in Miami-Dade, Monroe, and Collier counties (https://www.nps.gov/ever/learn/news/parkstatistics.htm). Boasting a diverse sub-tropical region of its own, the ENP houses 39 native orchid species.

Methods

Field methods

Study sites were selected based on prior knowledge of the species distribution and legal accessibility. Over the 4-year (2015–2019) study period, we visited a total of 29 sites with *T. undulatum* populations in Cuba across seven provinces including Artemisa, Cienfuegos, Matanzas, Mayabeque, Pinar del Rio, Sancti Spiritus, and Santiago. In this study, we defined a population of *T. undulatum* as a collection of all individuals that occur at a site. We surveyed plant communities at eight sites using transects at four provinces in Cuba: Matanzas, Mayabeque, Pinar del Rio, and Sancti Spiritus. A single transect was also surveyed at the ENP site in the USA. The transects range 499 km in the distance from each other with a median of 216 km. The identity of each host tree species for every *T. undulatum* encountered was documented at all sites. Non-host species were also documented along the transects.

Population and plant community sampling via transects

At each site where plant community sampling was possible, a 1-km non-linear transect was set-up where *T. undulatum* occurrence was deemed representative of the site. Most of these transects were along informal forest trails, including the one at the ENP. Once we encountered *T. undulatum*, we would search all trees within a 5-m radius for additional individuals. This approach was taken to maximize the probability of locating *T. undulatum* individuals for the orchid's population study (not presented here). A transect ended when it reached 1 km in length. Both host and non-host trees, shrubs, and lianas were identified as species for the entire transect length. Shrubs and lianas were included in the plant community study because they were occasional hosts of *T. undulatum* (pers. obs.). Diameter at breast height (DBH) of the host and the height at which the individual *T. undulatum* was found were recorded. In addition, abundance of host and non-host species were categorized into the following five categories within the transects: (1) very abundant, with 15 or more individuals, (2) moderately abundant, between 11 and 14 individuals, (3) somewhat abundant, between 6 and 10 individuals, (4) occasional presence, between 3 and 5 individuals, and (5) species with a rare presence, 1–2 individuals within the study area. While the transects were not a random sample as they maximized inclusion of host species, they nonetheless generated reasonable quantification of host and non-host species diversity and relative abundance where *T. undulatum* occurred. For the nine plant communities where a transect was sampled, South Florida included, habitat description was based on vegetation types as defined by Borhidi (1991).

Data analyses

To assess the thoroughness of our sampling effort, we plotted in Cuba two species accumulation curves: one for all recorded tree species and another for just the orchid host species (Figure 3 a&b). Only plants that were identified to species level were plotted. Differences in mean host tree DBH and height frequencies at which *T. undulatum* occurred were compared among sites using one-way ANOVA in SPSS 26 (SPSS, Chicago, Illinois, USA). Host preference was

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evaluated both qualitatively and quantitatively. Qualitatively, host preference was evaluated in three ways to provide a range between liberal and conservative evaluation scenarios. The most inclusive interpretation for host preference includes as a host every species that has been observed with the presence of a *T. undulatum* across all study sites. An intermediate interpretation is provided by creating species-wide abundance categories for every plant recorded along the Cuban transects, as follows: (1) 10 or fewer individuals, (2) between 11 and 30 individuals, and (3) 31 or more individuals. We then classified the species with the least abundant score and being a host as preferred hosts. The third approach, also the most conservative, was to calculate a host proportion using the abundance of host species at the transect sites divided by the overall abundance for every plant species. This preference interpretation criterion used a host proportion equal to or greater than 0.5 occurrences for each species.

Quantitatively, for species that are identified as preferred hosts in the strictest sense, the total number of trees encountered for each species and the number that were observed as hosts was compared to the total number of trees of all species and the total that were hosts, using Chi-square tests (Vergara-Torres *et al.* 2010). The species must have been observed at a minimum of three times to be tested statistically. The significant p value was adjusted by Bonferroni method.

Results

Habitat and host species in Everglades National Park, Florida, USA

The ENP population site is known as a coastal transitional buttonwood woodland or hammock (TBH) with a calcite marl substrate and thin detritus layer at approximately 0.3 m elevation above sea level (25°10'18" N, 80°54'28" W) (Ross *et al.* 2000, Rutchey *et al.* 2006, Saha *et al.* 2009). Flooding at the site between May and October occurs between the open salt marsh and tropical hardwood hammock. Post-storm disturbances can cause an influx of sea water at the site (Saha *et al.* 2009, Saha *et al.* 2015). The ENP site consists of a predominant canopy of buttonwood trees, *Conocarpus erectus*, with occasional occurrence of other woody plants such as *Sideroxylon celastrinum* and *Randia aculeata*, and an understory of herbaceous plants including *Alternanthera flavescens*, *Chromolaena frustrata*, and *Dicliptera sexangularis* (Saha *et al.* 2015, Wendelberger 2016). The TBH habitat is considered a threatened habitat type and is shrinking due to increasing salinity and sea-level rise at the ENP (Saha *et al.* 2009). This vegetation type can also be found in shallow coastal regions of Cuba (Borhidi 1991), but we have not yet located populations of *T. undulatum* in these habitats (personal observations).

A total of 277 individuals of *T. undulatum* were documented on the 1-km transect at the ENP population site and all were found growing on the dominant canopy tree species, *C. erectus*. The heights above the ground where *T. undulatum* was attached varied between 0.41 and 4 m (average = 1.36 ± 0.6 SD meter height for N=158). Host tree DBH ranged between 6 and 100 cm (average = 31 ± 18.5 SD cm, N=151) (Table 3).

Habitats in Cuba

The general plant communities identified for the Cuban transect sites were Semi-deciduous Mogote Complex (MC), Tropical Semi-deciduous Forest (TSF), Lowland Seasonal Rainforest (LSR), and Wet Montane Forest (WMF), all occupying an exposed limestone karst (Borhidi 1991).

A Semi-deciduous Mogote Complex (MC) is a type of Tropical Karstic Forest with four subdivisions that are based on species richness, location on the island, canopy height, and precipitation. Two MC subdivisions visited within this study include the *Spatheloio-Gaussian* Forest and the *Thrinacion-Punctulatae* Forest. The latter is a species-poor forest found between the Habana and Mayabeque provinces at 200–600 m elevation, while the former is a species-rich deciduous forest found in the western mountains exhibiting high endemism (Borhidi 1991). The *Spatheloio-Gaussian* Forest site (MC 1) visited was found near a popular hiker's trail in Pinar del Rio (22°33'39" N, 83°49'58" W). The *Thrinacion-Punctulatae* Forest site (MC 2) transect was laid out near Ceiba Mocha, Mayabeque, on two small mogotes (limestone hills) surrounded by pasture (22°57'25"N, 81°46'05" W). The mogotes are steep and the rocky cliffs make it difficult for pastoral animals to climb and damage the vegetation.

The Tropical Semi-deciduous Forest (TSF) community is commonly found along coastal areas where seawater flooding is common. Sites on the coasts of Yaguajay, Sancti Spiritus (TSF 1) (22°16'03" N, 79°12'33" W) (Figure 4 a&b), and Cienega de Zapata, Matanzas (TSF 2, TSF 3) are a microphyllous community also known as *Coccolobeto-Buresertum* (22°15'56" N, 81°07'05" W and 22°13'14" N, 81°08'08" W respectively). At the Guanahacabibes National Park, Pinar del Rio site (TSF 4), the coastal forest is known for the microphyllous *Bombacopsi-Catalpetum* plant community (21°55'24" N, 84°28'33" W) (Borhidi 1991).

LSRs were historically widespread in Cuba, but most are now agricultural zones. The LSR that we visited, Comunidad 23, Sancti Spiritus, is a predominantly shade-coffee region with high epiphyte richness (21°52'06" N, 79°40'54" W) (pers. comm., Aliesky Gil Carballo). Our LSR transect was in a riparian area with limestone substrate that had not been converted to coffee plantations. Canopy trees in the LSR forest type can reach 40 m in height (Borhidi 1991).

WMF are characterized by elevation (above 800 meters), annual precipitation of 1,700–3,000 mm, and a 20–25 m high canopy layer. They are found in the mountains of central to eastern Cuba (Borhidi 1991). One WMF was visited in the Sancti Spiritus Province along a river near the Banao Biology Research station in Jarico (21°51'36" N, 79°34'48" W).

Sampling efforts and observations of host and non-host species in Cuba

A total of 246 plant species were identified across the eight Cuban transects, with 74 of them observed as hosts for a total of 1,021 *T. undulatum* (Table 1). The two MC sites had the highest recorded number of woody plant species and host trees with a total of 46 host and 160 non-host species between them (Figure 2 a&b). The most common host species at MC1 were *Adelia ricinella* and *Gymnanthes lucida* at MC2 comprising 10% [N=245] and 6% [N=222] of the host species, respectively. Thirteen percent of the orchids at MC1 that were found growing epilithically (growing on the limestone substrate) with a majority of orchids (62%) at MC2 were found to be epilithic.

The TSF sites combined had a total 37 host species and 118 non-host species. The most dominant host species recorded at each site were *Oxandra lanceolata* (12 % at TSF 1) [N=71], *Bucida buceras* (55% at TSF 2 [N=281] and 30% at TSF 3 [N=23]), and *Adelia ricinella* (33% at TSF 4 [N=74]). The WMF and LSR sites had

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Table 1. List of all observed host species for *T. undulatum*, host plant family, and vegetation types found at the Cuban and Florida transect sites. The "*" denotes a preferred host based on a species low abundance at sites, yet with the presence of a *T. undulatum* epiphyte (36 species). The "ψ" symbol is used to distinguish the strict interpretation of a preferred host species based on whether a plant species had an observed *T. undulatum* at a minimum of 50% of the time that species was encountered (13 species). Site vegetation where the host species were found is abbreviated with the following acronyms: Mogote Complex (MC), Wet Montane Forest (WMF), Semi-deciduous Mogote Complex (SMC), Tropical Semi-deciduous Forest (TSF), Buttonwood Hammock (BH), and Lowland Seasonal Rainforest (LSR). Following the host species name in brackets [C] means that the species is native to Cuba, [FL] native to Florida - USA and [E] for exotic.

Host species	Family	Vegetation type
Adelia ricinella L. [C]	Euphorbiaceae	TSF, LSR, MC
Albizia saman (Jacq) Merr. [E]	Fabaceae	WMF
Amphitecna latifolia A.H.Gentry [C,FL]*	Bignoniaceae	TSF
Annona glabra L. [C,FL]*	Annonaceae	TSF
Bucida buceras L. [C] ψ	Combretaceae	TSF, MC
Bucida sp.	Combretaceae	
Bursera simaruba Sarg. [C,FL]	Burseraceae	MC
Canella winterana Gaertn. [C,FL]*	Canellaceae	MC
Casearia sylvestris Sw. [C]*	Salicaceae	MC
Cecropia peltata L. [C]	Urticaceae	TSF
Cecropia sp.	Urticaceae	
Cedrela odorata L. [C]	Meliaceae	TSF, LSR
Cedrela sp.	Meliaceae	
Celtis trinervia Lam. [C]	Cannabaceae	TSF, MC
Chrysophyllum cainito L. [C]	Sapotaceae	
Chrysophyllum oliviforme L. [C,FL]	Sapotaceae	TSF
Chrysophyllum sp.	Sapotaceae	TSF
Citharexylum caudatum L. [C]*,ψ	Verbenaceae	TSF
Citharexylum spinosum L. [C,FL]*	Verbenaceae	TSF, MC
Citrus sp.	Rutaceae	
Clusia minor L. [C]*,ψ	Clusiaceae	MC
Clusia rosea Jacq. [C,FL]	Clusiaceae	
Clusia sp.*,ψ	Clusiaceae	TSF
Cojoba arborea (L.) Britton & Rose [C]*	Fabaceae	MC
Comocladia dentata Jacq. [C]	Anacardiaceae	MC
Conocarpus erectus L. [C,FL]	Combretaceae	BH
Cordia gerascanthus L. [C]	Boraginaceae	MC
Crescentia cujete L. [C] ψ	Bignoniaceae	TSF, MC, WMF
Cupania glabra Sw. [C,FL]	Sapindaceae	TSF
Damburneya coriacea Sw. [C,FL]	Lauraceae	
Drypetes lateriflora (Sw.) Krug & Urb [C,FL]*	Putranjivaceae	TSF
Erythroxylum areolatum L. [C]	Erythroxylaceae	MC
Erythroxylum confusum Britton [C]	Erythroxylaceae	TSF, MC
Erythroxylum havanense Jacq. [C]	Erythroxylaceae	TSF, MC
Eugenia farameoides A. Rich [C]*	Myrtaceae	TSF
Eugenia monticola (Sw.) DC [C]	Myrtaceae	MC
Exothea paniculata (Juss.) Radlk. [C,FL]*	Sapindaceae	TSF
Ficus americana Aubl. [C,FL]	Moraceae	
Ficus aurea Nutt. [C,FL]	Moraceae	MC
Ficus citrifolia Mill. [C,FL]	Moraceae	MC, WMF

(*Continued*)

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Table 1. (*Continued*)

Host species	Family	Vegetation type
Ficus maxima Mill. [C,FL]	Moraceae	MC
Ficus sp.*	Moraceae	TSF
Gaussia princeps H. Wendl [C]	Arecaceae	MC
Guaiacum officinale L. [C,FL]	Zygophyllaceae	TSF
Guapira obtusata (Jacq.) Little [C,FL]*	Nyctaginaceae	MC
Guazuma ulmifolia Lam. [C]	Malvaceae	TSF, LSR
Gymnanthes lucida Sw. [C,FL]	Euphorbiaceae	TSF, MC
Hebestigma cubense (Kunth) Urb. [C] Ψ	Fabaceae	MC
Hibiscus elatus Sw. [C]	Malvaceae	
Jacaranda caerulea (L.) J. St.-Hil. [C]	Bignoniaceae	TSF, MC
Licaria jamaicensis Kosterm Ex Leon & Alain [C]*	Lauraceae	WMF
Lonchocarpus domingensis (Pers.) DC. [C]	Fabaceae	TSF
Maclura tinctoria (L.) D.Don ex Steud. [C]*	Moraceae	TSF
Mangifera indica L. [E]	Anacardiaceae	
Microcycas calocoma (Miq.) A. DC. [C]*	Zamiaceae	MC
Nectandra coriacea (Sw.) Griseb. [C,FL]*	Lauraceae	TSF
Ouratea elliptica (A. Rich.) M. Gomez [C]*	Ochnaceae	MC
Oxandra lanceolata (Sw.) Baill. [C]	Annonaceae	MC, TSF
Pachira cubensis (A. Robyns) Fern. Alon [C]*	Malvaceae	MC
Paullinia fuscescens Kunth. [C]*	Sapindaceae	TSF
Persea americana Mill. [E]	Lauraceae	
Petesiodes clusiifolium (Sw.) Kuntze [C]*,Ψ	Primulaceae	WMF
Pisonia aculeata L. [C,FL]	Nyctaginaceae	MC
Plumeria obtusa L. [C]	Apocynaceae	MC
Psidium guajava L. [C]*,Ψ	Myrtaceae	TSF
Roystonea regia (Kunth) O.F. Cook [C,FL]	Arecaceae	WMF
Savia sessiliflora (Sw.) Willd. [C]	Phyllanthaceae	LSR, MC
Senna tenuifolia H.S. Irwin & Barneby [C]	Fabaceae	MC
Sideroxylon foetidissimum Jacq. [C,FL]	Sapotaceae	MC, WMF, TSF
Spondias mombin L. [C]	Anacardiaceae	
Spondias purpurea L. [C]*	Anacardiaceae	TSF
Stigmaphyllon sagraeanum A. Juss. [C]	Malpighiaceae	MC
Syzygium jambos (L.) Alston [E] Ψ	Myrtaceae	WMF
Tabebuia calcicola Britton [C]*,Ψ	Bignoniaceae	MC
Tabebuia leptoneura Urb. [C]	Bignoniaceae	TSF
Tabebuia sp.	Bignoniaceae	WMF
Thyana trifoliata (Poit.) Ham. [C]*,Ψ	Sapindaceae	LSR,MC
Trichilia hirta L. [C]	Meliaceae	TSF, MC
Urena lobata L. [C]*	Malvaceae	MC
Vitex divaricata Sw. [C]	Lamiaceae	TSF
Volkameria aculeata L. [C]*,Ψ	Lamiaceae	TSF
Tree (Unidentified) 1		
Liana (Unidentified) 1*		MC

(*Continued*)

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Table 1. (*Continued*)

Host species	Family	Vegetation type
Liana (Unidentified) 2*		MC
Liana (Unidentified) 3*		MC
Liana (Unidentified) 4*,Ψ		TSF
Liana (Unidentified) 5*		TSF
Liana (Unidentified) 6*		MC
Liana (Unidentified) 7*		MC
Vine (Unidentified) 1*		MC

the least host richness with totals of nine host species [N=71] and six [N=34], respectively. *Syzygium jambos* made up the most common host species (55%) at the WMF site. The most common host recorded at the LSR site was *Guazuma ulmifolia* making up 33% of the host tree diversity. Few orchids were found growing epilithic at the WMF site (6%) and none at the LSR site.

We identified 92 host species at the 29 sites across seven provinces in Cuba, from a total of N=1,095 host tree observations (Table 2). Twenty-three of the 92 host species documented are native to both Cuba and southern Florida. Species accumulation curves show that sampling effort on the Cuban transects plateaus for both all species and host species encountered (Figure 3 a&b).

Host tree DBH and orchid height on host tree

We recorded the heights of over 845 *T. undulatum* in the Cuban transects that ranged between 0.1 and 8 meters (Figure 1b). The lowest height that a *T. undulatum* was observed is for those orchids found on the ground (0 m). The MC 2 site had the lowest heights on a host which indicates where the *T. undulatum* germinated is 0.1 m for three host trees: *Bursera simaruba, Erythroxylum* sp., *Erythroxylum havanense*, and *Gymnanthes lucida*. The tallest that a *T. undulatum* was observed was on a *Bucida buceras* at 8 m at TSF 2 site. We measured 698 host tree DBH at the transects that ranged between 1 and 100 cm (Figure 1a). The largest DBH recorded was a *Ficus* sp. at 105 cm at TSF 3 site. The smallest host plants were recorded at MC 2 and measured 0.25 cm from a *Stigmaphyllon sagraeanum* and two *B. simaruba* plants at 0.6 and 0.65 cm. The mean DBH among and within the nine sites were statistically significant ($F_{8,803} = 40.14$, $P = 0.0014$) as well as the heights ($F_{8,937} = 18.31$, $P = 0.0014$). The most distinct sites with respect to DBH were the LSR, ENP, and WMF (Figure 2a) (Bonferonni post hoc; $P = 0.00139$) (Figure 1 a&b).

Host preferences

Our combined data from the eight transects show that *T. undulatum* was found growing on 74 species or 43% of the total species encountered (Table 1). Most species on the transects were found not to be hosts [N=171], although some were scored as very abundant (Table 2). The preferred host list generated using the intermediately conservative criteria includes a total of 36 species and the more exclusive preferred host list identifies 13 species (Table 1). Statistically, proportions of trees being hosts for all of the 13 species identified as preferred hosts using the strictest criterion were significantly higher than the overall proportion of trees being hosts with all species pooled. Specifically, for *Bucida buceras*, $\chi^2 = 116.7$, $P < 0.001$; for *Citharexylum caudatum*, $\chi^2 = 126.6$, $P < 0.000$; for *Clusia minor*, $\chi^2 = 52.4$, $P < 0.001$; for *Crescentia cujete*, $\chi^2 = 276.4$, $P < 0.001$; for *Hebestigma cubense*, $\chi^2 = 227.2$, $P < 0.001$; for *Petesiodes clusiifolium* ($\chi^2 = 52.4$, $P < 0.001$; for *Syzygium jambos*, $\chi^2 = 503.8$, $P < 0.001$; for *Thyana trifoliata*, $\chi^2 = 135.2$, $P < 0.001$; and for *Volkameria aculeata*, $\chi^2 = 99.5$, $P < 0.001$. The following were not subject to the chi-square tests because they violated the test assumptions, Clusia sp., Liana (unidentified 4), *Psidium guajava. Tabebuia calcicola.*

Discussion

Our study illustrates that *T. undulatum* has a large number of host species in its core distribution, and it showed preference on a few of them. This information can be used to inform conservation strategy of this threatened species at its northern most range, as we will discuss in detail below. Studies of this kind are rare in the tropics, especially on orchids, one of the most diverse plant families among tropical plants (Tremblay *et al.* 1998). There is often a lack of resources and time to study epiphytic species in their current ranges before stochastic events or other rapid environmental changes, which demand emergency rescue and translocation actions. In some cases, it is difficult to know where a fallen epiphyte came from and prior knowledge on host species would be helpful to such actions (Tremblay *et al.* 1998). Active restoration initiatives for anticipating threats to the population growth of endangered plants are often needed (Liu *et al.* 2015, Liu *et al.* 2020, Maschinski & Haskins 2012). Success of such actions varies depending on the species habitat limitations. Restoration initiatives may have a greater likelihood of success when out-planting occurs on trees of the right species and size, aided by a list of host trees with preference orders (Mujica *et al.* 2013, Segovia-Rivas *et al.* 2018, Tremblay *et al.* 1998, Yang *et al.* 2017). Collecting baseline information for understudied species, like *T. undulatum*, can provide alternative solutions for conservation planners.

Habitats of T. undulatum *as defined by hosts*

The most diverse habitat in terms of host species was the Mogote Complex (MC) sites, which also have the highest percentages of epilithic plants. The *T. undulatum* plants at the MC sites are found at higher elevations and are possibly protected from both flooding and herbivory by large grazing herbivores (i.e. goats and cattle) (Aukema *et al.* 2007). We observed many plants growing on the Mogote rocky ground. Some orchid species are known to grow and recruit on rocky substrates (Kendon *et al.* 2020, Yokoya *et al.* 2015), but we did not observe any protocorms or seedlings of *T. undulatum* growing on rocky surfaces or crevices during the course of our study as we had on host trees. Judging from the size of the plants on the ground, it is likely that they fell from

Table 2. List of all plant species (236 taxonomically confirmed species, 72 families) recorded at eight 1-km long survey sites across 4 provinces in Cuba. Included are whether or not the plant species was observed as a host, vegetation types that the species was observed in, and the average abundance of the species at the sites.

Species	Family	Vegetation Type	No. Transects Present	Avg. Transect Abundance	Host (Y/N)
Abrus precatorius L.	Fabaceae	MC	2	7.5	N
Acacia farnesiana (L.) Willd.	Fabaceae	LSR	1	10.0	N
Acacia tenuifolia (L.) Willd.	Fabaceae	LSR, MC	2	12.0	N
Adelia ricinella L.	Euphorbiaceae	LSR, TSF, MC	6	8.5	Y
Ageratina havanensis (Kunth) R.M.King & H.Rob.	Asteraceae	TSF	1	5.0	N
Albizia saman (Jacq.) Merr.	Fabaceae	WMF, LSR, MC	3	5.0	Y
Alibertia edulis (Rich.) A.Rich. Ex DC.	Rubiaceae	TSF	1	2.0	N
Allophylus cominia (L.) Sw.	Sapindaceae	TSF, MC	4	5.0	N
Alvaradoa amorphoides subsp. *psilophylla* (Urb.) Cronquist	Picramniaceae	TSF	1	10.0	N
Ampelocera cubensis Griseb.	Ulmaceae	TSF	1	2.0	N
Amphilophium crucigerum (L.) L.G.Lohmann	Bignoniaceae	LSR, MC	2	3.5	N
Amphitecna latifolia (Mill.) A.H.Gentry	Bignoniaceae	TSF	1	5.0	Y
Amyris balsamifera L.	Rutaceae	MC	2	3.5	N
Amyris elemifera L.	Rutaceae	MC	1	10.0	N
Ancistranthus harpochiloides (M.Gómez) Lindau	Acanthaceae	MC	1	14.0	N
Andira inermis (Wright) DC.	Fabaceae	TSF, MC	4	4.3	N
Annona glabra L.	Annonaceae	TSF	1	2.0	Y
Aristolochia bilabiata L.	Aristolochiaceae	MC	1	2.0	N
Aristolochia ringens Vahl	Aristolochiaceae	LSR	1	5.0	N
Ateleia gummifera (DC.) D.Dietr.	Fabaceae	TSF	1	5.0	N
Badiera propinqua Britton	Polygalaceae	TSF	1	2.0	N
Banisteriopsis pauciflora (Kunth) C.B.Rob.	Malpighiaceae	MC	1	5.0	N
Bignonia diversifolia Kunth	Bignoniaceae	TSF	1	2.0	N
Bomarea edulis (Tussac) Herb.	Alstromeriaceae	MC	1	2.0	N
Bourreria baccata Raf.	Boraginaceae	MC	1	10.0	N
Bucida buceras L.	Combretaceae	TSF, MC	3	17.7	Y
Bunchosia articulata Dobson	Malpighiaceae	TSF, MC	2	2.0	N
Bursera simaruba (L.) Sarg.	Burseraceae	WMF, LSR, TSF, MC	7	5.6	Y
Calophyllum brasiliense var. *antillanum* (Britton) Standl.	Clusiaceae	WMF, LSR, TSF	3	8.0	N
Calycophyllum candidissimum (Vahl) DC.	Rubiaceae	LSR	1	2.0	N
Calyptranthes pallens Griseb.	Myrtaceae	MC	1	2.0	N
Calyptronoma occidentalis (Sw.) H.E.Moore	Arecaceae	WMF, LSR	2	2.0	N
Canavalia nitida (Cav.) Piper	Fabaceae	MC	2	2.0	N
Canella winterana (L.) Gaertn.	Canellaceae	LSR, MC	2	3.5	Y
Capsicum annuum L.	Solanaceae	MC	1	5.0	N
Casearia aculeata Jacq.	Salicaceae	WMF, LSR, TSF, MC	6	4.5	N
Casearia guianensis (Aubl.) Urb.	Salicaceae	TSF, MC	3	5.0	N
Casearia praecox Griseb.	Salicaceae	TSF	1	2.0	N
Casearia sylvestris Sw.	Salicaceae	MC	1	5.0	Y
Catalpa macrocarpa (A.Rich.) Ekman ex Urb.	Bignoniaceae	TSF	1	5.0	N

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Table 2. (*Continued*)

Species	Family	Vegetation Type	No. Transects Present	Avg. Transect Abundance	Host (Y/N)
Cecropia peltata L.	Urticaceae	WMF, LSR, TSF, MC	5	3.2	N
Cedrela odorata L.	Meliaceae	LSR, TSF, MC	5	2.6	Y
Ceiba pentandra (L.) Gaertn.	Malvaceae	TSF, MC	3	2.0	N
Celtis iguanaea (Jacq.) Sarg.	Cannabaceae	TSF	1	2.0	N
Celtis trinervia Lam.	Cannabaceae	TSF, MC	4	5.5	Y
Centrosema virginianum (L.) Benth.	Fabaceae	MC	1	5.0	N
Chiococca alba (L.) Hitchc.	Rubiaceae	LSR, TSF, MC	5	5.0	N
Chrysobalanus icaco L.	Chrysobalanaceae	TSF	1	5.0	N
Chrysophyllum oliviforme L.	Sapotaceae	WMF, TSF, MC	4	4.3	Y
Cissus obovata Vahl	Vitaceae	MC	1	5.0	N
Cissus verticillata (L.) Nicolson & C.E.Jarvis	Vitaceae	WMF, TSF, LSR,MC	6	5.0	N
Citharexylum caudatum L.	Verbenaceae	TSF	1	10.0	Y
Citharexylum spinosum L.	Verbenaceae	MC	2	5.0	Y
Citrus reticulata Blanco	Rutaceae	MC	1	5.0	N
Clusia minor L.	Clusiaceae	MC	1	5.0	Y
Clusia rosea Jacq.	Clusiaceae	WMF, LSR, MC	4	3.5	Y
Clusia sp.	Clusiaceae	TSF	1	2.0	Y
Cojoba arborea (L.) Britton & Rose	Fabaceae	MC	1	5.0	Y
Comocladia dentata Jacq.	Anacardiaceae	LSR, TSF, MC	4	8.5	Y
Cordia bullata var. *globosa* (Jacq.) Govaerts	Boraginaceae	TSF	1	2.0	N
Cordia collococca L.	Boraginaceae	LSR, TSF	2	3.5	N
Cordia gerascanthus L.	Boraginaceae	WMF, LSR, TSF, MC	6	8.5	Y
Crescentia cujete L.	Bignoniaceae	WMF, LSR, TSF, MC	5	7.8	Y
Crossopetalum uragoga (Jacq.) Kuntze	Celastraceae	MC	1	2.0	N
Croton lucidus L.	Euphorbiaceae	MC	1	19.0	N
Cubanola daphnoides (Graham) Aiello	Rubiaceae	MC	1	5.0	N
Cupania americana L.	Sapindaceae	LSR, TSF, MC	3	5.0	N
Cupania glabra Sw.	Sapindaceae	WMF, LSR, MC, TSF	4	6.3	Y
Cupania juglandifolia A.Rich.	Sapindaceae	TSF, MC	2	5.0	N
Cynophalla flexuosa (L.) J.Presl	Capparaceae	MC, TSF	4	5.0	N
Dalbergia ecastaphyllum (L.) Taub.	Fabaceae	TSF	2	7.5	N
Dendropanax arboreus (L.) Decne. & Planch.	Araliaceae	LSR, TSF, MC	3	5.0	N
Dioscorea sp.	Dioscoreaceae	TSF	1	2.0	N
Dioscorea sp.	Dioscoreaceae	MC	1	2.0	N
Diospyros caribaea (A.DC.) Standl.	Ebenaceae	MC	1	2.0	N
Diospyros crassinervis (Krug & Urb.) Standl.	Ebenaceae	TSF, MC	2	3.5	N
Drypetes alba Poit.	Putranjivaceae	TSF	2	5.0	Y
Drypetes ilicifolia (DC.) Krug & Urb.	Putranjivaceae	MC	1	2.0	N
Ehretia tinifolia L.	Boraginaceae	MC	1	5.0	N
Erythrina sp.	Fabaceae	LSR	1	5.0	N
Erythroxylum areolatum L.	Erythroxylaceae	TSF, MC	5	6.8	Y
Erythroxylum confusum Britton	Erythroxylaceae	TSF, MC	3	5.0	Y

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Table 2. (*Continued*)

Species	Family	Vegetation Type	No. Transects Present	Avg. Transect Abundance	Host (Y/N)
Erythroxylum havanense Jacq.	Erythroxylaceae	LSR, TSF, MC	7	11.9	Y
Eugenia axillaris (Sw.) Willd.	Myrtaceae	MC, TSF	2	7.5	N
Eugenia farameoides A. Rich.	Myrtaceae	TSF	1	5.0	Y
Eugenia ligustrina (Sw.) Willd.	Myrtaceae	TSF	1	5.0	N
Eugenia monticola (Sw.) DC.	Myrtaceae	TSF, MC	5	8.8	Y
Eugenia rocana Britton & P.Wilson	Myrtaceae	MC	1	2.0	N
Exothea paniculata (Juss.) Radlk.	Sapindaceae	MC, TSF	2	3.5	Y
Ficus americana Aubl.	Moraceae	MC	1	2.0	N
Ficus aurea Nutt.	Moraceae	LSR, TSF, MC	5	5.0	Y
Ficus citrifolia Mill.	Moraceae	WMF, TSF, MC	4	3.5	Y
Ficus crassinervia Desf. ex Willd.	Moraceae	TSF, MC	3	3.0	N
Ficus maxima Mill.	Moraceae	LSR, TSF	2	5.0	N
Ficus membranacea C.Wright	Moraceae	WMF, LSR, MC	5	4.4	Y
Ficus sp.	Moraceae	TSF	1	5.0	Y
Forestiera rhamnifolia Griseb.	Oleaceae	MC	2	2.0	N
Fridericia podopogon (DC.) L.G.Lohmann	Bignoniaceae	TSF, MC	2	3.5	N
Gaussia princeps H.Wendl.	Arecaceae	MC	1	14.0	Y
Genipa americana L.	Rubiaceae	LSR	1	5.0	N
Ginoria americana Jacq.	Lythraceae	LSR	1	10.0	N
Gouania lupuloides (L.) Urb.	Rhamnaceae	LSR, MC	2	10.0	N
Gouania polygama (Jacq.) Urb.	Rhamnaceae	LSR, MC	2	10.0	N
Guapira obtusata (Jacq.) Little	Nyctaginaceae	MC	1	2.0	Y
Guarea guidonia (L.) Sleumer	Meliaceae	WMF, MC	2	5.0	N
Guazuma ulmifolia Lam.	Malvaceae	WMF, LSR, TSF, MC	4	5.5	Y
Guettarda calyptrata A.Rich.	Rubiaceae	MC	2	5.0	N
Guettarda combsii Urb.	Rubiaceae	TSF	1	2.0	N
Gymnanthes lucida Sw.	Euphorbiaceae	TSF, MC	5	11.6	Y
Hamelia patens Jacq.	Rubiaceae	TSF	1	2.0	N
Hebestigma cubense (Kunth) Urb.	Fabaceae	MC	1	14.0	Y
Heteropteris laurifolia (L.) A.Juss.	Malpighiaceae	LSR	1	5.0	N
Hibiscus elatus Sw.	Malvaceae	LSR, TSF	2	7.5	Y
Hirtella triandra Sw.	Chrysobalanaceae	WMF	1	2.0	N
Hura crepitans L.	Euphorbiaceae	MC	1	5.0	N
Hypelate trifoliata Sw.	Sapindaceae	MC	1	2.0	N
Hyperbaena cubensis (Griseb.) Urb.	Menispermaceae	MC	1	2.0	N
Ilex cassine L.	Aquifoliaceae	TSF	1	5.0	N
Ipomea tiliacea (Willd.) Choisy	Convolvulaceae	MC	2	5.0	N
Ipomoea nil (L.) Roth	Convolvulaceae	MC	2	5.0	N
Ipomoea sp.	Convolvulaceae	LSR	1	5.0	N
Ipomoea tiliacea (Willd.) Choisy	Convolvulaceae	LSR	1	10.0	N
Ixora ferrea (Jacq.) Benth.	Rubiaceae	LSR	1	5.0	N
Jacaranda caerulea (L.) J.St.-Hil	Bignoniaceae	TSF, MC	2	6.0	Y

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Table 2. (*Continued*)

Species	Family	Vegetation Type	No. Transects Present	Avg. Transect Abundance	Host (Y/N)
Jacquinia aculeata Druce	Theophrastaceae	LSR	1	5.0	N
Jacquinia curtisii (Britton) Lepper & J.E.Gut.	Theophrastaceae	TSF	1	2.0	N
Jatropha integerrima Jacq.	Euphorbiaceae	MC	1	5.0	N
Juglans jamaicensis subsp. *insularis* (Griseb.) H. Schaarschm.	Juglandaceae	MC	1	2.0	N
Koanophyllon villosum (Sw.) R.M.King & H.Rob	Asteraceae	MC, LSR	2	10.0	N
Lantana aculeata L.	Verbenaceae	MC	1	10.0	N
Lantana involucrata L.	Verbenaceae	TSF	1	5.0	N
Lasiacis divaricata (L.) Hitchc.	Poaceae	LSR, TSF, MC	3	4.0	N
Lasiacis sloanei (Griseb.) Hitchc.	Poaceae	MC	1	2.0	N
Leucothrinax morrisii (H.Wendl.) C.Lewis & Zona	Arecaceae	MC	1	10.0	N
Licaria jamaicensis Kosterm. ex Leon & Alain	Lauraceae	WMF	1	5.0	Y
Lonchocarpus sericeus (Poir.) DC.	Fabaceae	WMF, LSR, TSF	4	5.0	Y
Luehea speciosa Willd.	Malvaceae	LSR	1	5.0	N
Lysiloma latisiliquum (L.) Benth.	Fabaceae	TSF	1	2.0	N
Maclura tinctoria (L.) D.Don ex Steud.	Moraceae	TSF	1	2.0	Y
Malpighia cubensis Kunth	Malpighiaceae	TSF	1	2.0	N
Malpighia sp.	Malpighiaceae	LSR	1	5.0	N
Mangifera indica L.	Anacardiaceae	LSR	1	5.0	N
Marcgravia rectiflora Triana & Planch.	Marcgraviaceae	WMF, LSR	2	2.0	N
Margaritaria nobilis L.f.	Phyllanthaceae	TSF	1	2.0	N
Matelea oblongata (Griseb.) Woodson	Apocynaceae	MC	1	2.0	N
Melicoccus bijugatus Jacq.	Sapindaceae	MC	1	2.0	N
Melothria pendula L.	Cucurbitaceae	MC	1	5.0	N
Metastelma linearifolium A.Rich	Apocynaceae	MC	1	5.0	N
Metopium brownei (Jacq.) Urb.	Anacardiaceae	MC	1	5.0	N
Miconia sp.	Melastomataceae	LSR	1	5.0	N
Microcycas calocoma (Miq.) A.DC.	Zamiaceae	MC	1	5.0	Y
Microgramma heterophylla (L.) Wherry	Polypodiaceae	MC	1	5.0	N
Momordica charantia L.	Cucurbitaceae	WMF	1	5.0	N
Morinda royoc L.	Rubiaceae	LSR, TSF, MC	6	7.5	N
Mucuna urens (L.) Medik.	Fabaceae	WMF, LSR	2	3.5	N
Nectandra coriacea (Sw.) Griseb.	Lauraceae	TSF	1	10.0	Y
Orthosia scoparia (Nutt.) Liede & Meve	Apocynaceae	MC	1	2.0	N
Ouratea elliptica (A.Rich.) M.Gomez	Ochnaceae	MC	1	2.0	Y
Oxandra lanceolata (Sw.) Baill.	Annonaceae	LSR, TSF, MC	5	12.4	Y
Pachira cubensis (A.Robyns) Fern. Alonso	Malvaceae	TSF, MC	2	2.0	Y
Parthenocissus quinquefolia (L.)Planch.	Vitaceae	TSF	1	2.0	N
Passiflora multiflora L.	Passifloraceae	MC	2	3.5	N
Passiflora suberosa L.	Passifloraceae	LSR, TSF, MC	3	5.0	N
Paullinia fuscescens Kunth.	Sapindaceae	TSF	1	2.0	Y
Peperomia rotundifolia (L.) Kunth	Piperaceae	MC	1	2.0	N

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Table 2. (*Continued*)

Species	Family	Vegetation Type	No. Transects Present	Avg. Transect Abundance	Host (Y/N)
Petesiodes clusiifolium (Sw.) Kuntze	Primulaceae	WMF	1	5.0	Y
Petitia domingensis Jacq.	Lamiaceae	TSF	1	5.0	N
Philodendron consanguineum Schott	Araceae	WMF, MC	3	5.0	N
Philodendron hederaceum (Jacq.) Schott	Araceae	MC	1	2.0	N
Philodendron lacerum (Jacq.) Schott	Araceae	WMF, LSR, MC	3	5.0	N
Picramnia pentandra Sw.	Picramniaceae	TSF, MC	5	10.8	N
Pinochia corymbosa (Jacq.) M.E.Endress & B.F.Hansen	Apocynaceae	MC	1	5.0	N
Piper aduncum var. *ossanum* (C.DC.) Saralegui	Piperaceae	MC	1	5.0	N
Piper articulatum C.DC.	Piperaceae	MC	1	5.0	N
Pisonia aculeata L.	Nyctaginaceae	LSR, TSF, MC	4	9.8	Y
Platygyna hexandra (Jacq.) Müll. Arg.	Euphorbiaceae	MC, WMF	3	5.0	N
Pleopeltis polypodioides (L.) E.G.Andrews & Windham	Polypodiaceae	LSR, MC	2	2.0	N
Plumbago zeylanica L.	Plumbaginaceae	MC	1	10.0	N
Plumeria obtusa L.	Apocynaceae	LSR, TSF, MC	4	10.0	Y
Pouteria dominigensis (C.F.Gaertn.) Baehni	Sapotaceae	MC	1	2.0	N
Prockia crucis P.Browne ex L.	Salicaceae	TSF	1	2.0	N
Psidium guajava L.	Myrtaceae	TSF	1	2.0	Y
Psiguria pedata (L.) R.A.Howard	Cucurbitaceae	MC	1	5.0	N
Psychotria horizontalis Sw.	Rubiaceae	MC	1	10.0	N
Psychotria nervosa Sw.	Rubiaceae	MC	1	10.0	N
Quadrella cynophallophora (L.) Hutch.	Capparaceae	TSF, MC	2	5.0	N
Rauvolfia nitida Jacq.	Apocynaceae	TSF	1	2.0	N
Rhytidophyllum exsertum Griseb.	Gesneriaceae	MC	1	19.0	N
Rondeletia odorata Jacq.	Rubiaceae	LSR	1	5.0	N
Roystonea regia (Kunth) O.F.Cook	Arecaceae	WMF, LSR, TSF, MC	4	4.3	Y
Sabal maritima (Kunth) Burret	Arecaceae	TSF	1	5.0	N
Salix caroliniana Michx.	Salicaceae	TSF	1	2.0	N
Sapium glandulosum (L.) Morong	Euphorbiaceae	WMF	1	14.0	N
Savia sessiliflora (Sw.) Willd.	Phyllanthaceae	LSR, TSF, MC	3	12.7	Y
Securidaca elliptica Turcz.	Polygalaceae	LSR, TSF, MC	6	4.0	N
Senna spectabilis (DC.) H.S.Irwin & Barneby	Fabaceae	LSR	1	10.0	N
Serjania diversifolia (Jacq.) Radlk.	Sapindaceae	TSF	1	2.0	N
Serjania subdentata Juss. ex Poir.	Sapindaceae	LSR, MC	3	5.0	N
Sideroxylon foetidissimum Jacq.	Sapotaceae	WMF, TSF, MC	6	5.0	Y
Sideroxylon salicifolium (L.) Lam.	Sapotaceae	MC	1	5.0	N
Smilax domingensis Willd.	Smilacaceae	WMF, TSF, MC	3	5.0	N
Smilax havanensis Jacq.	Smilacaceae	LSR, TSF, MC	4	4.3	N
Solandra longiflora Tussac	Solanaceae	MC	1	2.0	N
Solanum nitidum Ruiz & Pav.	Solanaceae	MC	1	10.0	N
Spathodea campanulata P.Beauv.	Bignoniaceae	WMF	1	10.0	N
Spondias mombin L.	Anacardiaceae	LSR	1	5.0	N

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Table 2. (*Continued*)

Species	Family	Vegetation Type	No. Transects Present	Avg. Transect Abundance	Host (Y/N)
Spondias purpurea L.	Anacardiaceae	TSF	1	2.0	Y
Sterculia apetala (Jacq.) H.Karst.	Malvaceae	MC	1	5.0	N
Stigmaphyllon sagraeanum A.Juss.	Malpighiaceae	LSR, MC	3	5.0	Y
Swietenia mahagoni (L.) Jacq.	Meliaceae	TSF	1	5.0	N
Syzygium jambos (L.) Alston	Myrtaceae	WMF, LSR	2	24.5	Y
Tabebuia angustata Britton	Bignoniaceae	LSR, TSF	3	5.0	Y
Tabebuia calcicola Britton	Bignoniaceae	MC	1	2.0	Y
Tabebuia leptoneura Urb.	Bignoniaceae	TSF	2	5.0	N
Tabebuia myrtifolia (Griseb.) Britton	Bignoniaceae	MC	1	2.0	N
Tabebuia shaferi Britton	Bignoniaceae	TSF	1	5.0	N
Tabernaemontana alba Mill.	Apocynaceae	TSF, MC	2	5.0	N
Talipariti elatum (Sw.) Fryxell	Malvaceae	WMF	1	14.0	Y
Tecoma stans (L.) Juss. ex Kunth	Bignoniaceae	LSR, MC	2	9.5	N
Thyana trifoliata (Poit.) Ham.	Sapindaceae	LSR, MC	3	3.0	Y
Trichilia havanensis Jacq.	Meliaceae	WMF, LSR, TSF, MC	4	7.3	N
Trichilia hirta L.	Meliaceae	LSR, TSF, MC	4	8.8	Y
Trichostigma octandrum (L.) H.Walter	Phytolaccaceae	MC	1	10.0	N
Turbina corymbosa (L.) Raf.	Convolvulaceae	LSR, MC	3	10.0	N
Turnera ulmifolia L.	Passifloraceae	MC	1	5.0	N
Unidentified Liana #1		MC	1	5.0	Y
Unidentified Liana #2		MC	1	5.0	Y
Unidentified Liana #3		MC	1	5.0	Y
Unidentified Liana #4		TSF	1	2.0	Y
Unidentified Liana #5		MC	1	5.0	Y
Unidentified Liana #6		MC	1	5.0	Y
Unidentified Liana #7		MC	1	5.0	Y
Unidentified Vine		MC	1	5.0	Y
Urena lobata L.	Malvaceae	MC	1	5.0	Y
Urera baccifera (L.) Gaudich. ex Wedd.	Urticaceae	LSR, MC	3	5.0	N
Varronia bullata L.	Boraginaceae	LSR, TSF, MC	3	6.7	N
Vernonanthura menthaefolia (Poepp. ex Spreng.) H.Rob.	Asteraceae	MC	1	5.0	N
Volkameria aculeata L.	Lamiaceae	TSF	1	10.0	Y
Wedelia rugosa Greenm.	Asteraceae	MC	1	5.0	N
Zanthoxylum caribaeum Lam.	Rutaceae	TSF	2	3.5	N
Zanthoxylum elephantiasis Macfad.	Rutaceae	TSF	1	2.0	N
Zanthoxylum fagara (L.) Sarg.	Rutaceae	TSF, MC	2	3.5	N
Zanthoxylum martinicense (Lam.) DC.	Rutaceae	WMF, LSR, MC	3	5.0	N
Zuelania guidonea (Sw.) Britton & Millsp.	Salicaceae	TSF, MC	3	2.0	N

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Table 3. The range and average (± SD) diameter at breast height (DBH) and height of the *T. undulatum* observed was recorded for the nine 1-km transect sites across habitat types.

Site name	Habitat type	DBH (cm) Average±SE	Height above ground (m) Average±SE
MC 1	MC	12.7^{cde} ± 16.6	2.81^{f} ± 1.6
MC 2	MC	6.3^{e} ± 4.3	1.96^{eg} ± 1.6
TSF 1	TSF	7.7^{e} ± 3.8	2.94^{bcdf} ± 1.3
TSF 2	TSF	14.5^{cde} ± 10.1	2.21^{d} ± 1.0
TSF 3	TSF	19.9^{bcdef} ± 11.1	$2.29^{abcdefg}$ ± 0.9
TSF 4	TSF	16^{cde} ± 9.6	2.65^{bcdf} ± 1.1
LSR	LSR	41.3^{a} ± 16.1	3.1^{cf} ± 2.1
WMF	WMF	20.8^{f} ± 11.6	2.55^{bcdf} ± 2.1
ENP	BH	31^{b} ± 18.5	1.36^{g} ± 0.6

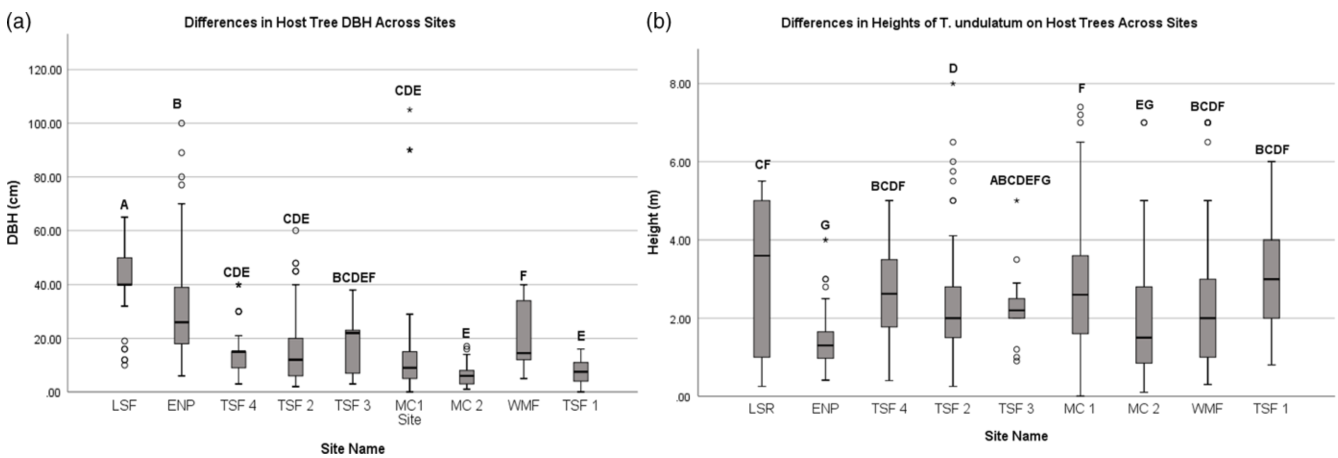

Figure 1 a&b. The range and average (± SD) diameter at breast height (DBH) and height of the *T. undulatum* observed was recorded for all nine 1-km transect sites across habitat types in Cuba and Florida, USA.

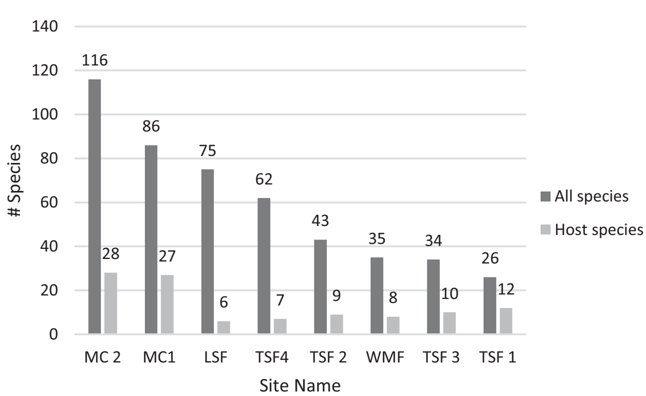

Figure 2 a&b. Species richness for the following a) total species found across eight transect sites in Cuba and b) *T. undulatum* host species found across eight transect sites in Cuba.

the host trees nearby. In habitats that experience periodic floodings, such as coastal TSF, BH, or LSR sites, *T. undulatum* individuals are unlikely to survive while on the ground.

The three sites with the lowest host species richness were the ENP, WMF, and LSR sites. The LSR and WMF habitats are particularly impacted by human presence. The LSR habitats are considered the most common habitat type in Cuba and are seen as ideal for agricultural usage, which makes these sites severely impacted by human presence (Borhidi 1991). Two of eight hosts documented at the WMF site are listed as invasive, including the most common host tree at the site, *Syzygium jambos*, which is found along rivers and waterways (CABI 2021). The ENP site is periodically flooded by salt water, dominated by *Conocarpus erectus* trees throughout, and the population runs between an open saltwater marsh with no canopy tree species as well as manmade canals skirted by dense *Rhizophora mangle*. It comes as no surprise that *C. erectus* is the only host within this population due to a lack of alternative woody species in the area with a relatively open canopy. *Conocarpus erectus* was not reported in any of the Cuban vegetation assays and therefore not reported as a host in any of the *T. undulatum* populations in Cuba.

Trichocentrum undulatum is likely not microsite limited when germinating since such a wide-scale usage of tree species and growing locations were observed in Cuba. However, in southern Florida, coastal hammocks near the sole existing population were explored in the search for more populations of *T. undulatum* but none have been found (pers. obs.). There may be pollination and seed limitations caused by *T. undulatum*'s deceptive pollination strategy and the lower pollinator availability in the southern Florida

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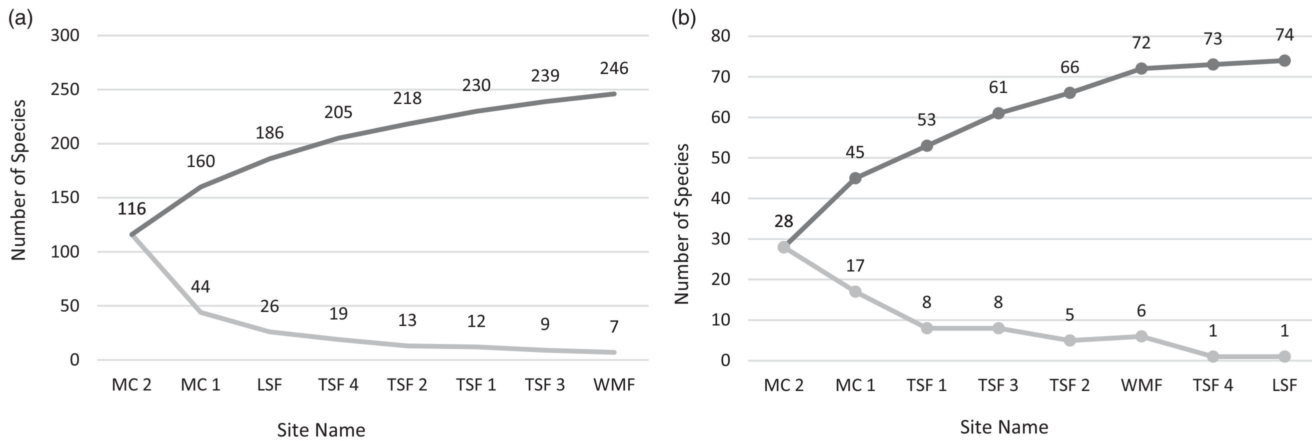

Figure 3 a&b. Species accumulation curves for the following a) total species found across 8 transect sites in Cuba and b) *T. undulatum* host species found across 8 transect sites in Cuba. The darker line represents the compounding total of new species and the lighter colored line represents the number of new species encountered at subsequent sites.

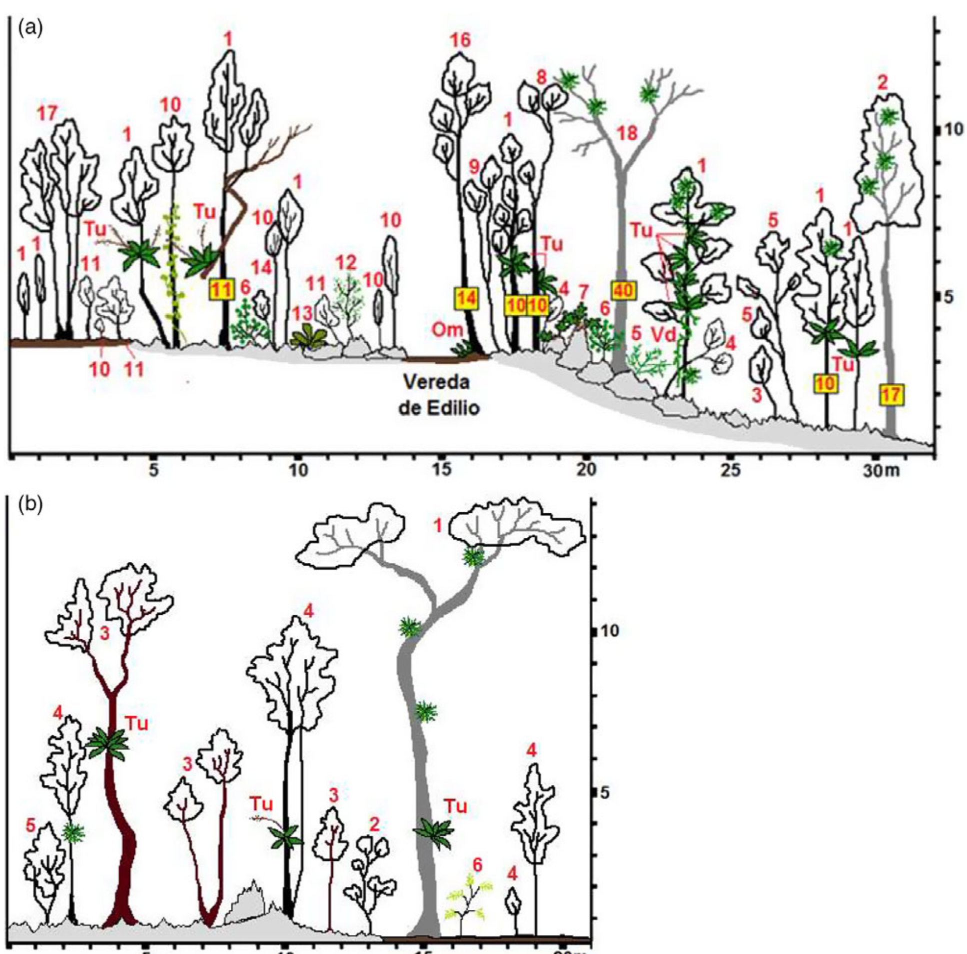

Figure 4 a&b. Two profiles were drawn from within transects in August of 2018 off the trail of La Vereda de Edilio, Sancti Spiritus, Cuba where demographic information was collected for *Trichocentrum undulatum* at a tropical semideciduous forest in Jobo Rosado protected area (N 22°29614 W -79°22910). *Courtesy of MSc. Armando Falcón Méndez, Biologist, Specialist of Parque Nacional Caguanes, CSASS, CITMA.* **a**) The woody species have numerical denominations while smaller herbaceous species are an acronym of the first letter of both genus and species: 1 - *Oxandra lanceolata*, 2 - *Zanthoxylum caribaeum*, 3 - *Adelia ricinella*, 4 - *Picramnia pentandra*, 5 - *Olyra latifolia*, 6 - *Erythroxylum havanense*, 7 - *Philodendron lacerum*, 8 - *Cupania glabra*, 9 - *Casearia aculeata*, 10 - *Eugenia axillaris*, 11 - *Amyris balsamifera*, 12 - *Eugenia ligustrina*, 13 - *Anthurium cubense*, 14 - *Cordia gerascanthus*, 15 - *Trichilia hirta*, 16 - *Exothea paniculata*, 17 - *Gossypiospermum praecox*, 18 - *Cedrela odorata*, 19 - *Bignonia diversifolia*, Tu - ***Trichocentrum undulatum***, Om - *Oeceoclades maculata*, Tf - *Tillandsia fasciculata*, and Vd - *Vanilla dilloniana*. **b**) The woody species have numerical denominations while smaller herbaceous species are an acronym of the first letter of both genus and species: 1 - *Cedrela odorata*, 2 - *Adelia ricinella*, 3 - *Sideroxylon foetidissimum*, 4 - *Oxandra lanceolata*, 5 - *Picramnia pentandra*, 6 - *Acacia tenuifolia*, Tu - ***Trichocentrum undulatum***, and Tf - *Tillandsia fasciculata*.

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population (Ackerman *et al.* 1996, Turnbull *et al.* 2000). The presence of specialized herbivores as well as high herbivory rates found in the southern Florida population exacerbates fruit set and limits seed production, so although the habitat is there, the seeds may not be (Borrero *et al.* 2018, Higgins and Gann 2007). Varied mycorrhizal diversity between host trees and habitat types is also likely to be important, particularly because epiphytic orchids may depend on mycorrhizal fungi for water in harsh and dry conditions (Gowland *et al.* 2013, Kartzinel *et al.* 2013, Rock-Blake *et al.* 2017, Yoder *et al.* 2000). Bark rugosity, seasonal light penetration through canopy, as well as throughfall of nutrients adds yet more dimensions of complexity that may have an effect to some extent on host tree choices (Callaway *et al.* 2002, Hirata *et al.* 2008, Sayago *et al.* 2013, Zarate-Garcia *et al.* 2020).

Implications for management

This study is the first to evaluate the differences among habitats for populations of *T. undulatum* across its distribution. Our study is also a reflection of our best effort in understanding the orchid's hosts and vegetation communities in Cuba while access to natural areas is limited. Due to the diversity of host tree species, substrates, elevations, and plant species richness across the Cuban sites, we are certain that the Cuban *T. undulatum* populations are not host-specific (Ackerman *et al.* 2007, Nieto-Blázquez *et al.* 2017). The restricted southern Florida population occurred in mangroves with very limited tree diversity, and only one species, *Conocarpus erectus*, serves as a host tree for *T. undulatum*. It is not uncommon for specialist species to express stress characteristics on the leading edges of their distributions due to lower habitat quality (Franco *et al.* 2006). Yet there may be hope for *T. undulatum* since the wide range of hosts found in the core range overlaps with southern Florida (23 out of the 69 identified Cuban native host species are also native to Florida, USA). Our host list recommendations suggest that particular species be targeted in translocation and conservation projects in Florida, beginning with the species that are both native as well as noted as preferred, followed by intermediately preferred, and finally the more inclusive hosts. Unfortunately, there are no species in the most preferred host list that are native to mainland Florida, an indication that the habitats in South Florida are marginal.

The most similar habitat type in southern Florida to the sites observed in Cuba is the Tropical Hardwood Hammock or Rockland Hammock (G2/S2 Global/State Rank), in which 25 species have been recorded that are *T. undulatum* host trees in Cuba (Institute for Regional Conservation 2021). A listing of "exemplary" Rockland Hammocks that may be adequate planting sites for future projects focused on *T. undulatum* includes: Dagny Johnson Key Largo Hammock Botanical State Park, John Pennekamp Coral Reef State Park, and Lignumvitae Key Botanical State Park (all in Monroe County) as well as Matheson Hammock, Royal Palm Hammock, and Everglades National Park in Miami-Dade county (Florida Natural Areas Inventory 2010). Management of host tree species within orchid distribution is encouraged since available host trees can be a limiting factor for epiphytic orchid populations (Migenis & Ackerman 1993). Although sites in Cuba did have healthy individuals growing on the ground, recommendations for ground planting will not be made for future conservation work due to the flooding risk, ease of potential poaching, as well as increasing herbivory potential.

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Competing Interests. The authors declare none.

Ethical Statement. None.

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